Field Guide to Classify Biological Soil Crusts for Ecological Site Evaluation

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Introduction

Biological soil crusts (also known as microbiotic, cryptobiotic, cryptogamic, or microphytic soil crusts, or here simply biocrusts) are crucial components of terrestrial ecosystems. These crusts are essential for aggregating mineral particles at the soil surface (West, 1990; St. Clair & Johansen, 1993; Evans & Johansen, 1999; Belnap et al., 2001; Belnap et al., 2003). They contain microbial communities of diverse taxa, such as bryophytes, lichens, eukaryotic algae, cyanobacteria, fungi and/or bacteria, and their byproducts. The microscopic biocrust communities function ecologically to: stabilize soils, fix nitrogen and carbon, regulate water cycling in an out of soils, capture dust, accumulate organic matter, supply nutrients to vascular plants, enhance and/or reduce seedling establishment, promote chemical and physical weathering, provide wildlife habitat, and regulate soil food web interactions (for examples see West, 1990; Johansen, 1993; Evans & Johansen, 1999; Belnap et al., 2001; Johansen & Schubert, 2001; Shepherd et al., 2002; Zaady & Bouskila, 2002; Darby et al., 2007, Williams et al., 2012).

Different ecological sites favor certain crust taxa, which, when dominant, form recognizable morphological/functional crust community types (Eldridge and Rosentreter, 1999; Belnap et al., 2001; Pietrasiak, 2005, Pietrasiak et al., 2011, 2013, 2014). The community types can then be classified based upon these dominant taxa because they display characteristic morphologies (i.e., thalli, coloration, microtopography, dry and moist morphologies). As the result of their surface morphologies, community composition, and crust development (successional state), biocrust community types vary in their ecosystem function, particularly in regard to soil stability, nitrogen fixation or carbon fixation rates, and dust capture (Williams et al., 2012, Pietrasiak et al., 2013). Thus, each ecological site will function overall differently depending on which crust communities prevail.

In contrast to those in cold deserts, biocrusts in the semiarid and arid ecosystems of southern California can be inconspicuous. They are commonly thin and embedded under a layer of gravel, within rock crevices, or beneath shrub canopies. This field guide will aid in the identification of biocrust community types in southern California. Specifically, it may applied in the following USDA-NRCS MLRA Land Resource Regions: California Coastal Plain (C19), Southern California Mountains (C20), Sierra Nevada Mountains (D22a), Southern Nevada Basin and Range (D29), Mojave Desert (D30), and the Lower Colorado Desert (D31).

Key to Biocrust Community Type Classification in the Field

The key is structured dichotomously. Identification requires dry soil surface conditions.

1) no soil surface consolidation; loose soil………………………………….no soil crust

2) surface aggregate lifts off the soil surface by inserting a knife or finger into the soil; fine biological filaments absent, i.e. distinct filaments or "danglies" cannot be seen with the naked eye; slakes quickly in water…....……..........non-biological crust, p. 5

3) weak consolidation; soft and breaking easily when lifted up with fingers; clear presence of fine filaments as seen with the naked eye, i.e. distinct "danglies" often with soil particles attached (under stereo microscope these are cyanobacterial, fungal, algal filaments)..incipient algal/fungal crust, p. 8

4) strong consolidation; not breaking by light mechanical up and down shaking of crust aggregates being held between the index finger and thumb; embedded under a distinct, approximately 1-cm thick surface layer of litter or sand (i.e. embedded); fungal hyphae visible …………………………………..………………..………fungal crust, p. 10

5) strong consolidation; not embedded; inconspicuous coloration….light algal crust p. 12

6) strong consolidation; not embedded; soil surface has conspicuous darkened coloration; no lichen and/or moss thalli ……………………………………..dark algal crust, p. 15

7) strong consolidation; not embedded; crust with conspicuous lichen thalli appearing as small disk- or ribbon-like structures; no leaf-like structures; thallus surface not turning green when moistened; fine rhizine structures and/or hyphae visible underneath thallus……………..lichen crust, p. 18

a) algae layer coloration bright green after lichen thalli moistened with water and cut in cross section; ………………....................green algae lichen crust, p. 18

b) algae layer coloration blue-green or entire lichen thalli gelatinous and brownish green after lichen thalli moistened with water and cut in cross section; ……………………………………..........cyanobacteria lichen crust, p. 18

8) strong consolidation; not embedded; crust with conspicuous moss thalli appearing leaf-like in structure; surface turning green when moistened in the field…...bryophyte crust, p. 22

   a) individual moss thalli not visible with naked eye but detectable with 10x hand lens; appearing as smooth velvet-like green, brown or dark brown blankets on the soil surface; thalli with branchlike filaments……...smooth moss crust, p. 22

   b) individual bryophyte phylli clearly visible with naked eye; thalli not greater than 5 mm tall; appearing brown or dark brown when dry and green to dark green when moistened.………………… …. …….roughened moss crust, p. 22

   c) individual bryophyte phylli clearly visible with naked eye; phylli < 5 mm tall; appearing blackened……………………....................…..dark moss crust, p. 22

   d) individual bryophyte phylli > 5 mm tall; hairlike extensions as long as phyllus; resulting in a fuzzy surface………..................................hairy moss crust, p. 22

   e) byophyte phylli “V-shape” or “Y-shape”, flat, and appressed closely on soil surface; dark brown, sometimes with black margins, when dry; olive green to green when moist………………......……………………...liverwort crust, p. 22

Crust Type Classification

Non-biological crusts

Inorganic soil crusts are common soil surface features in arid and semiarid ecosystems. Physical or chemical processes, or a combination of both, lead to their formation (Belnap et al., 2001).

Physical crusts

In general, these compact soil crusts can be classified into structural and depositional physical crusts (Valentin 1991, Valentin and Bresson, 1992). Structural crusts form *in situ* (Valentin and Bresson, 1992). They commonly develop after rain-splash breaks up surface aggregates and causes slaking. Often, vesicular porosity can be observed. Depositional crusts form from the settling out of soil particles, that were transported to a topographical low point by runoff or by the deposition of particles in standing water (Valentin and Bresson, 1992). Fine stratification or platy structure results (Figure 1). Depositional crust formation may be linked to natural wetting and drying events. In addition, anthropogenic land uses such as use of heavy agricultural machinery, irrigation techniques, or livestock can cause a depositional crust to develop. In these cases, the anthropogenic impacts to the land lead to compaction of the soil surface layers, greater sediment transport in overland flow, and ponding at topographic low points where particles settle out to form a laminar depositional crust (Valentin 1991).

Chemical crusts

The most common chemical soil crusts develop on the surface of soils with high salt content. When saline water evaporates at the soil surface, salt crystals precipitate and are left behind on the surface (Figure 2). At a first sight, salt crusts can closely resemble biocrusts. However, no biological filaments (hyphae or algal filaments) can be detected by viewing a chemical soil crust with a 5x hand lens. Salt crusts on soils are not to confused with halophilic biofilms or mats found on salt pans and playas. Such salt loving microbial communities are not associated with soil material but with playa or pan sediment and often contain diverse biofilms often dominated by photosynthetic active cyanobacteria and purple bacteria and their heterotrophic associates (Nübel et al., 1999, Navaro et al., 2009).

Ecological functions

The often sealed crust surface of non-biological soil crusts is associated with reduced water infiltration and increased run off (Valentin 1991). Seedling establishment and root penetration may be impeded (Wood et al., 1982). However, plant growth may be promoted in adjacent non-crusted areas if these areas receive additional water from runoff (Wood et al., 2005).

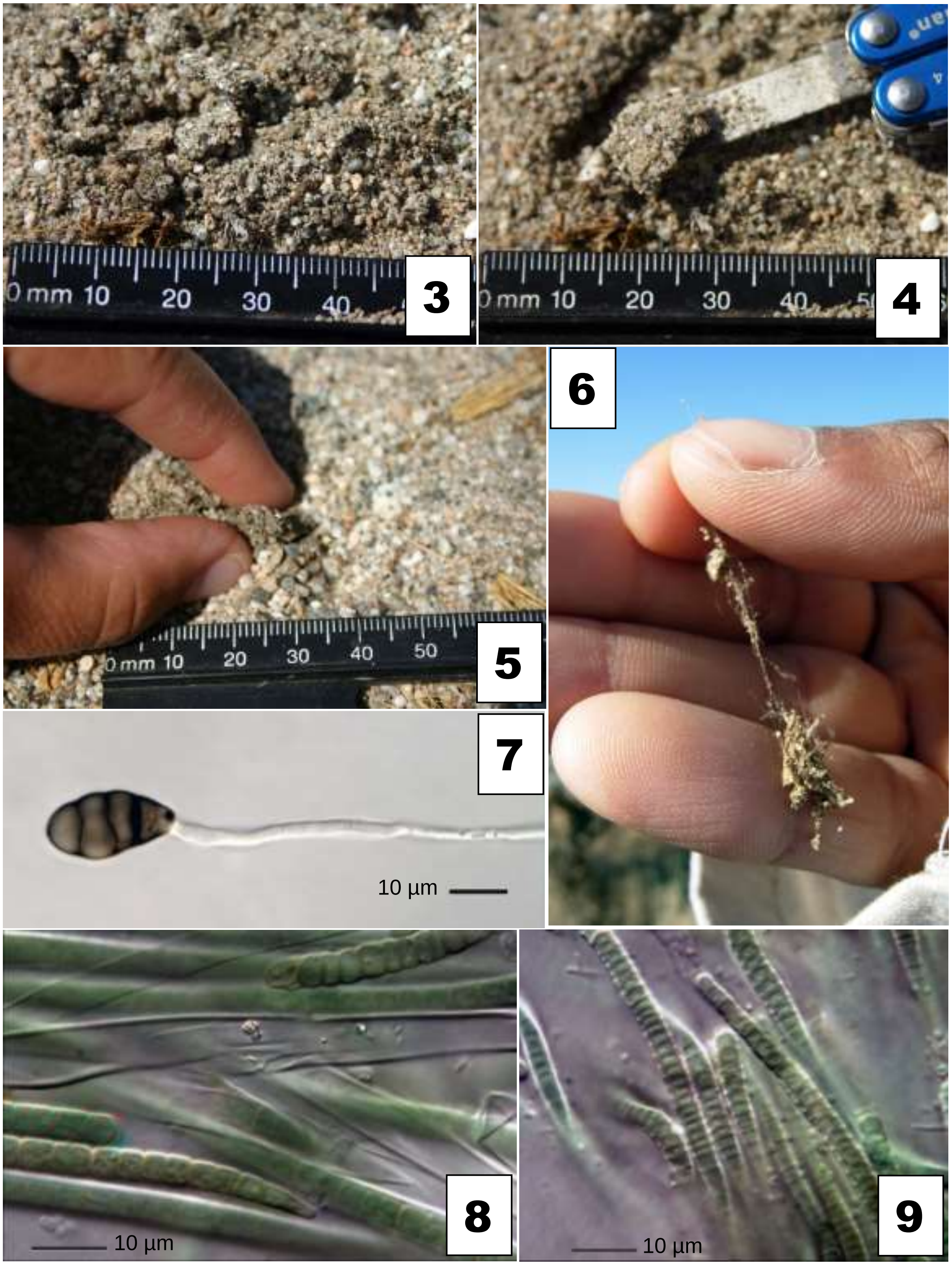
Figures 1-2. 1) Physical crust showing distinct platy structure. 2) Chemical salt crust with close up showing salt crystals.

Incipient algal/fungal crusts

Algal crusts contain both, eukaryotic algae (Phylum Chlorophyta; Classes Bacillariophyceae, Xanthophyceae, and Eustigmatophyceae in the Phylum Ochrophyta) and prokaryotic algae (Phylum Cyanobacteria). All algal crusts are considered subterraneous crusts; i.e., their photosynthetic tissue is found below the soil surface intermixed with the mineral soil particles. This contrasts with crusts that are dominated by lichens and mosses, which have the photosynthetic tissue above ground (Belnap et al., 2003). Incipient crusts are usually found in disturbed sites or on geomorphically active land surfaces. They appear as very soft crusts and are weakly consolidated, i.e., they break very easily when lifted and mechanically shaken (Figures 3-5). Yet, they are held together by distinct cyanobacterial and/or fungal filaments (Figure 6). Biodiversity and biomass of this crust type is low (Figure 7). Morphological simple filamentous cyanobacteria of the genus *Microcoleus* (Figure 8), the genus *Symplocastrum*, members of the family Leptolyngbyaceae (example in Figure 9), and various coccoid green algae species are commonly associated with this crust.

Ecological functions

The ecological role of incipient crusts is marginal (Pietrasiak et al., 2013). Carbon fixation, nutrient mineralization, and decomposition are minimal, and nitrogen fixation is not detectable (nitrogen-fixing organisms require a stable soil surface). Incipient crusts at a site in the Mojave Desert fixed only 0.79 µmol CO_2 m^{-2} s^{-1}. Soil aggregate stability to water erosion is low and incipient crusts generally disintegrated relatively rapidly in water within 30 seconds of immersion (Pietrasiak et al., 2013). However, incipient crusts can develop quickly after a disturbance when soil moisture becomes available if the soil already contains or the ground surface efficiently traps propagules. This crust then provides surface stabilization to allow subsequent colonization by other crust community members that require initially stabilized soil surfaces (Belnap et al., 2003).



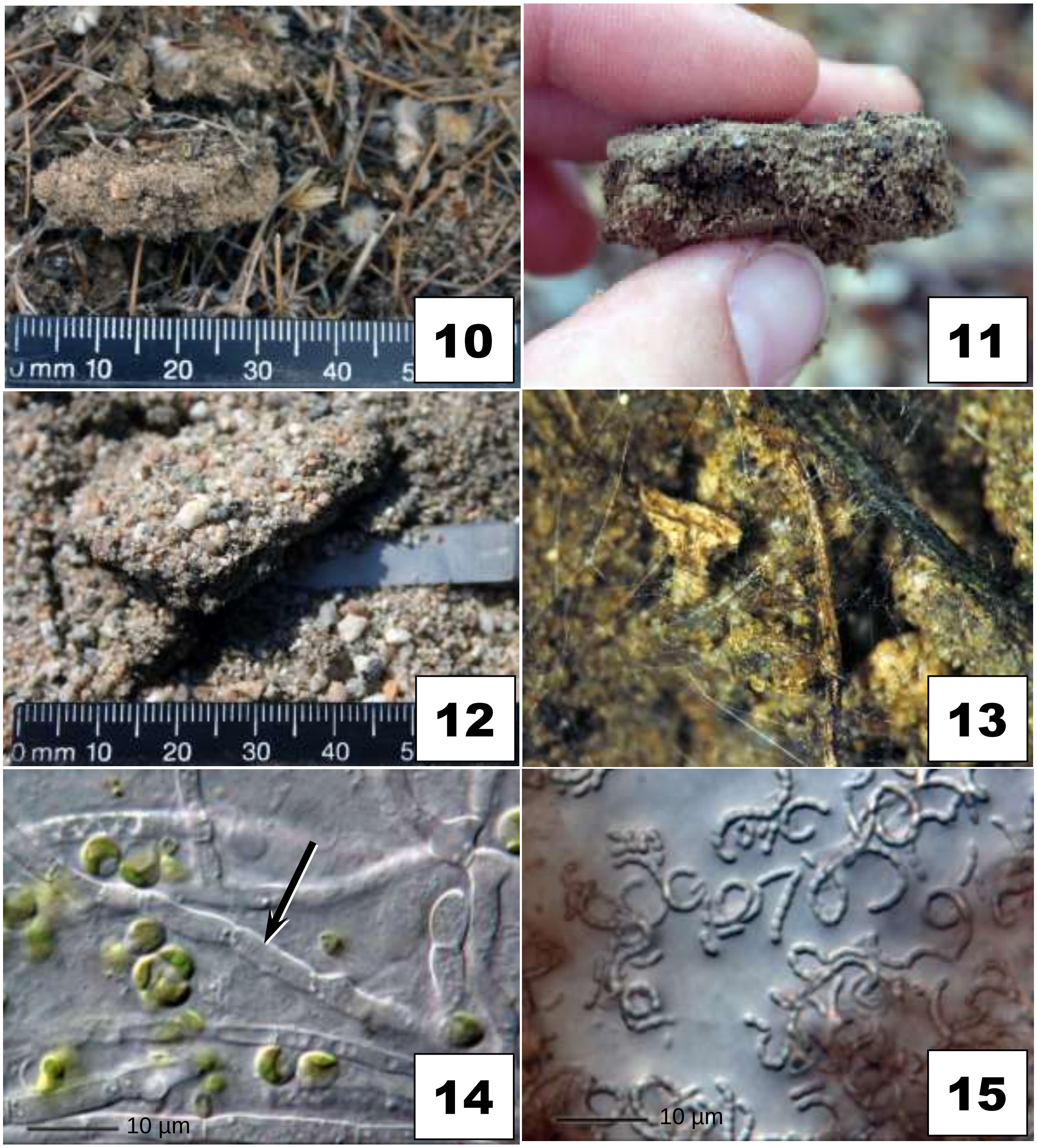
Figures 3-9. 3-5) Soft appearance of weakly consolidated incipient algal/fungal crusts; 6) fungal hyphae with attached soil particles; 7) fungal hypha with sporangium found in incipient crust on desert pavement; 8) *Microcoleus steenstrupii;* 9) Leptolyngbyaceae sp.

Fungal crusts

Fungi can form 1-2 cm thick crusts underneath a 1-cm-thick litter layer (Figures 10 and 11). In some instances, they may be buried under a 1-cm-thick sandy layer (Figure 12). Most likely, those crusts have been previously exposed at the soil surface as algal crusts with a minor fungal component. After a disturbance, these surface crusts become buried by deposits of water-or wind-borne sediment, the photosynthetic organisms disappeared from the community and only fungi and bacteria remain as dominant community components (Belnap and Eldridge 2003).

Ecological functions

Fungal crusts can play an important role in soil aggregate formation and stability (Belnap et al., 2001, 2003) (Figure 13). Pietrasiak et al., (2013) reported a high degree of soil aggregate stability for these crusts with aggregates holding together after 5 min of being immersed in water and withstanding mechanical dipping. In addition, decomposition, mineralization, and heterotrophic biomass contributions can be high. In contrast, no significant photosynthetic fixation of carbon can be detected in these buried crusts since the photosynthetically active members require light. Occasionally, a few motile eukaryotic algae species can be associated with these crusts. The ability to sporadically use organic carbon as an energy source as well as to move through moist substrate may allow these algae to survive in the buried crusts. Nitrogen fixation depends on the presence of free-living heterotrophic bacteria and can vary from not detectable to 6.1×10^{-5} nmol N_2 m^{-2} h^{-1} (Zaady et al., 1998, Pietrasiak 2012, Pietrasiak et al., 2013). Fungal crusts have been overlooked in past crust studies and their biodiversity and ecological functions remain understudied (Figures 14 and 15).



Figures 10-15. 10 and 11) Fungal crust under litter with strong consolidation; 12) fungal crust underneath a sand layer; 13) fungal hyphae network stabilizing soil particles; 14) translucent fungal hyphae (below arrow) of an unidentified fungus under 1000x magnification; 15) unique bacteria populations associated with fungal crusts.

Light algal crusts

Light algal crusts, together with fungal crusts, are the most inconspicuous crust types. The coloration is similar to that of the non-biological crusted soil surfaces (Figure 16 and 17). Hence, one must check the surface soil for aggregation as well as for the development of subterraneous biological filaments. The dominant community members are prokaryotic cyanobacteria and eukaryotic algae. Occasionally after rain events fast growing green algal colonies add reddish or greenish tints to crust surfaces (Figures 18-20). The surface morphology of light algal crusts can range from smooth to rugose and thickness varies from 1 mm up to 2 cm.

Together with incipient algal crusts, light algal crusts have the quickest recovery potential after disturbance. In addition, these crusts are commonly found in areas with harsher environmental conditions (hotert and drier). They are adapted to lower moisture requirements and desiccation by virtue of their extracellular polysaccharide production. These polysaccharides promote water retention and prolong cell hydration (Belnap and Gardner 1993). Polysaccharides have also been linked to soil particle trapping and binding due to their sticky consistency (Belnap and Gardner 1993, Williams et al., 2012). However, dust trapping capacity of algal crusts is considered to be relatively low in comparison to the morphologically more complex lichen and moss crusts (Williams et al., 2012).

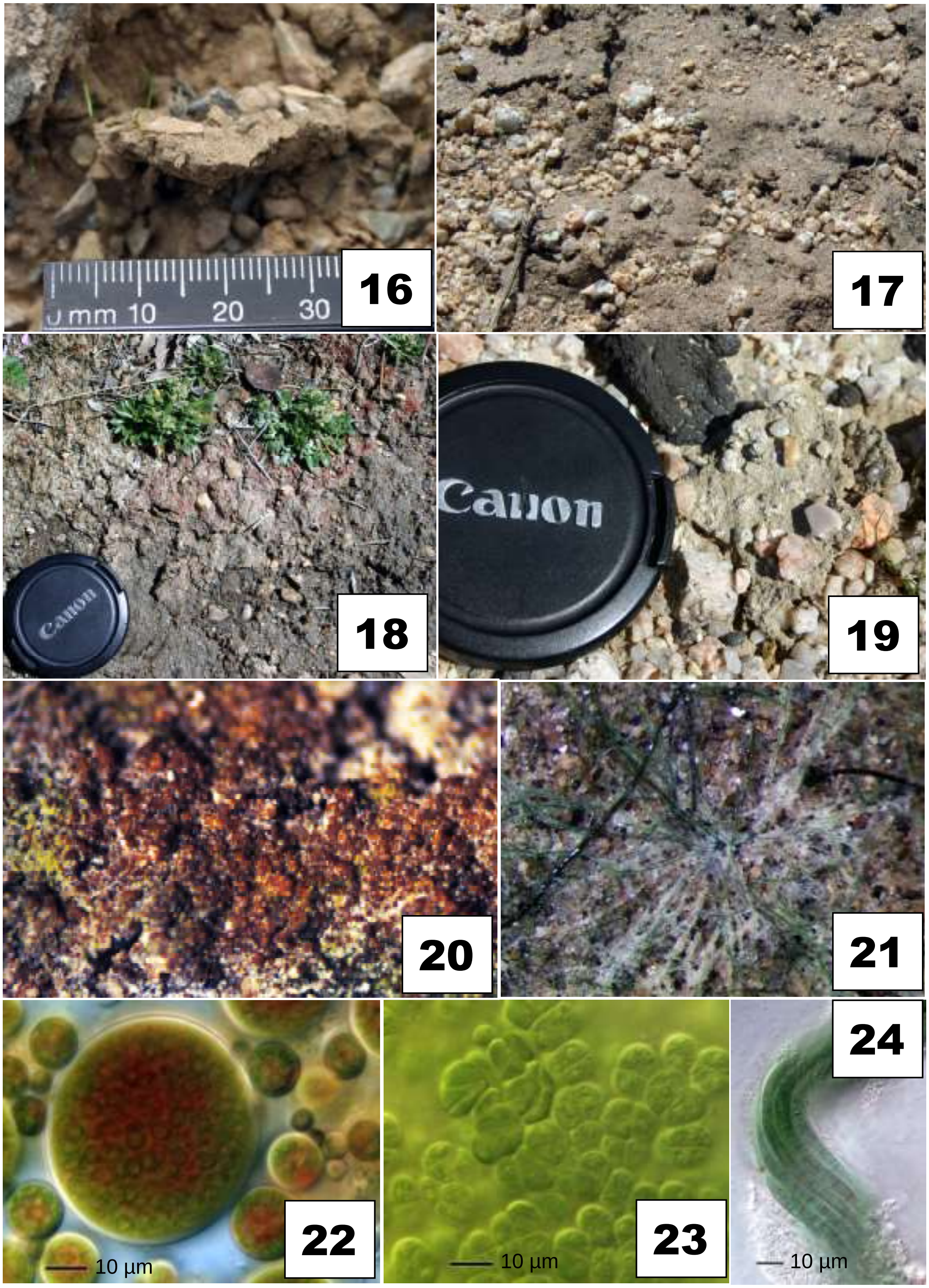
Ecological functions

The carbon input for light cyanobacterial/eukaryotic algal crusts is low and has been generally estimated to range 0.4-2.3 gC m^{-2} per year (Lange 2003). Rates of carbon fixation range from 0.11 to 3.03 µmol CO_2 m^{-2} s^{-1}. Carbon fixation rates from light algal crusts in the Mojave Desert averaged about 1.01 µmol CO_2 m^{-2} s^{-1} (Pietrasiak 2012, Pietrasiak et al., 2013). Nitrogen fixation varies greatly, from minimal rates of 7.3 nmol N_2 m^{-2} h^{-1} detected in the Colorado Plateau, U.S. (Belnap 1996) to 5.5 x 10^{-6} nmol N_2 m^{-2} h^{-1} in temperate dry climates in China (Su et al., 2011). Nitrogen fix rates reported from

Mojave Desert light algal crusts average about 7.3 x 10^{-2} nmol N_2 m^{-2} h^{-1} (Pietrasiak 2012, Pietrasiak et al., 2013).

Light algal crusts may be important for soil aggregate stability, imparting moderate to high aggregate stabilities (Pietrasiak et al., 2013). Biodiversity of eukaryotic soil algae in these crusts is often very high, commonly including genera such as *Actinochloris*, *Bracteacoccus, Chlorella, Chlorococcum, Scenedesmus, Chlorosarcinopsis*, *Eustigmatos, Stichococcus, Myrmecia*, *Trebouxia*, *Heterococcus*, *Hantzschia*, *Luticola*, and *Pinnularia (Flechtner et al., 2013, Pietrasiak unpublished data)*. However, fast growing morphologically simple, filamentous cyanobacteria make up most of the photosynthetic biomass and often include the genera *Microcoleus, Symplocastrum, Trichocoleus, Oculatella*, *Nodosilinea*, *Pseudophormidium,* and *Phormidesmis* (Figures 21-24).

Figures 16-24. 16 and 17) Inconspicuous light algal crusts; 18 and 19) red and green tinted crust after winter rain; 20) close up of red colored soil crust showing green algae colonies; 21) cyanobacteria *Microcoleus vaginatus* filaments forming extensive network on soil surface; 22) green algae *Bracteacoccus* sp. at 1000x; 23) green algae *Chlorosarcinopsis* sp. at 1000x; 24) *Microcoleus vaginatus* at 1000x.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Dark algal crusts

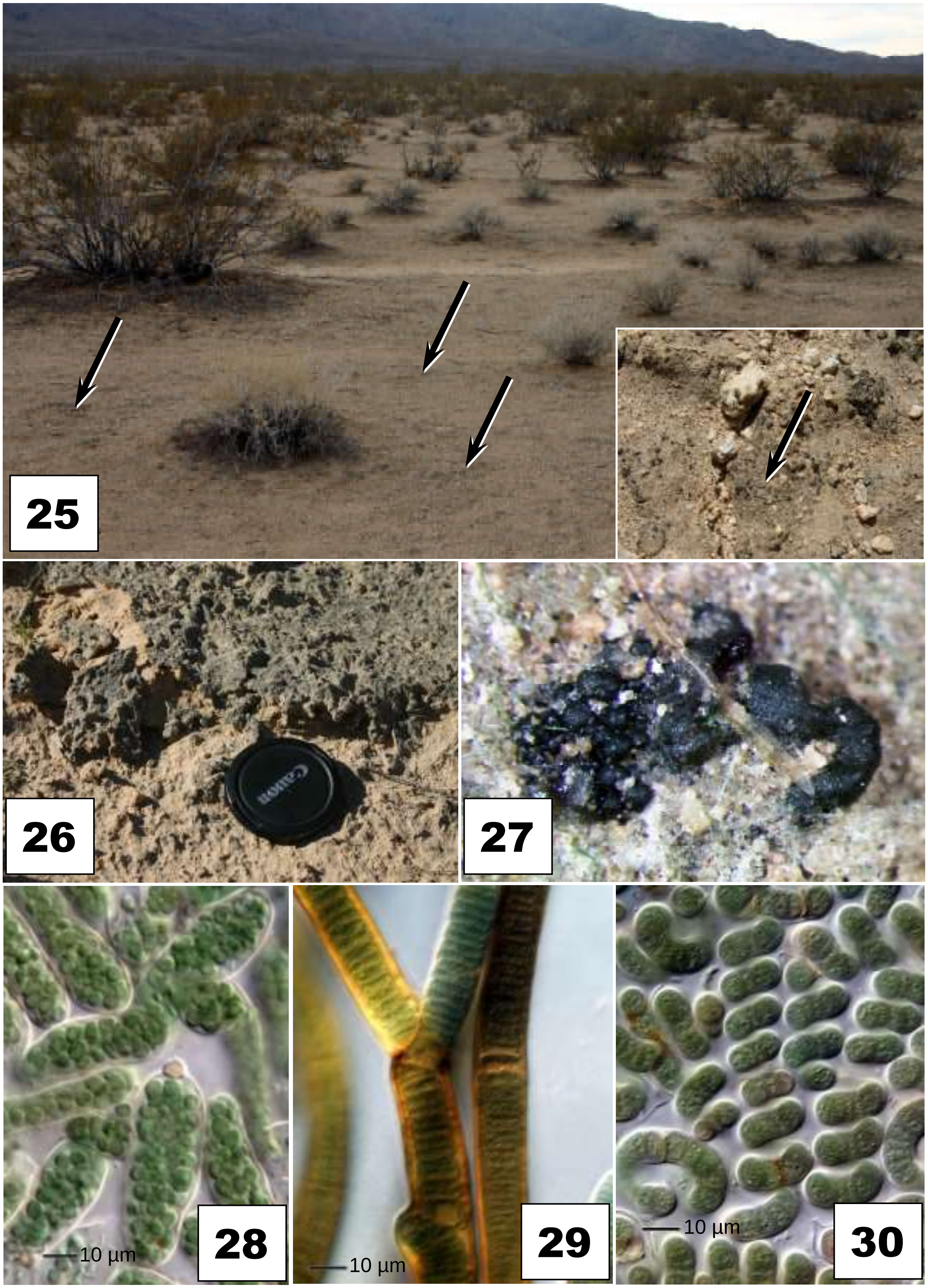
Dark algal crusts conspicuously darken the soil surface (Figures 25 and 26). The darkening is caused by the greater abundance of free-living nitrogen-fixing cyanobacteria that establish directly on the crust surface (Figures 27-30). Genera of soil cyanobacteria capable of nitrogen fixing include *Nostoc*, *Hassallia*, *Scytonema*, *Calothrix*, *Spirirestris*, and *Mojavia*. These cyanobacteria are equipped with dark sun-screen pigments (Figure 29) which in combination cause the soil surface to appear gray-black color. Dark algal crusts reveal lighter coloration just beneath the dark surface layer when crusts are broken apart.

Ecological functions

Dark algal crusts are the best-developed algal crust type with regard to biomass, carbon and nitrogen fixation capacity, and soil aggregate stability (Pietrasiak 2012). Although, two studies reported low nitrogen fixation values for a site in the Chihuahuan Desert (3.0 nmol N_2 m^{-2} h^{-1}) and a site in the Colorado Plateau (6.0 nmol N_2 m^{-2} h^{-1}), most studies report values ranging from 1.4 x 10^{-3} nmol N_2 m^{-2} h^{-1} to 2.3 x 10^{-6} nmol N_2 m^{-2} h^{-1} (reviewed in Pietrasiak 2012). Carbon fixation rates for this crust type are moderate and range from 0.19 µmol CO_2 m^{-2} s^{-1} (Colorado Plateau) to 5.00 µmol CO_2 m^{-2} s^{-1} (Central American savanna). Dark algal crusts from a site in the Mojave Desert fixed an average of 1.78 µmol CO_2 m^{-2} s^{-1} (Pietrasiak 2012).

Soil aggregate stability is high as crusts hold together strongly after being immersed in water for 5 min and being exposed to mechanical dipping in a water column. Additionally, these crusts can also significantly reduce albedo by darkening the soil surface, resulting in greater absorption of solar radiation, and increased soil temperature. This could affect seedling germination of vascular plants in early spring.

Figures 25-30. 25) Darkening of the soil surface (arrows) with close up of dark algal crust; 26) blackened crust on sandy soil; 27) close up ofthe nitrogen-fixing cyanobacteria *Nostoc* sp.; 28) cyanobacteria *Nostoc* sp. with heterocytes at 1000x; 29) cyanobacteria *Hassallia* sp. with sunscreening pigments in sheath material at 1000x; 30) the rare heterocytous cyanobacteria *Spirirestris rafaelensis* at 1000x.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Lichen crusts

A lichen is a symbiotic association between a fungal and an algal symbiont. The fungal component provides sunscreen protection, nutrients, and substrate anchorage for the photobiont (= alga). The algal component provides carbohydrates for the fungus. Lichen taxonomy is based on the fungal component. The photobiont typically has a species name as well and may be important for lichen identification at a coarse taxonomic level (i.e., genus and family level). In contrast to all previous crust types, lichens and mosses have their photosynthetic tissue on or above soil surface (Belnap et al., 2003). However, thick networks of rhizomorphs and hyphae extend into the soil.

Green algal lichen crust (phycolichen crust)

Phycolichens are associations of fungi and eukaryotic green algae. If one cuts a cross section through a phycolichen thallus it is commonly stratified into two layers: the whitish fungal layer with a dark sunscreen skin and a green algal layer. On the outside, the thallus is in general brighter in pigmentation (brown, red, white, yellow colors, Figures 36-40) and exhibits a wide array of morphological complexity. Common morphologies vary from squamulous (corn flake-like with the thallus margin upraised, *Clavicidium lacinulatum*, *Placidium squamulosum, Psora decipiens*, Figures 36 and 39), foliose (intricate leafy thallus, *Physconia sp.*, *Xanthoparmelia,* sp., Figure 38), fruticose (morphologically complex thallus such as podetia of *Cladonia*) or crustose (*Sarcogyne mitziae, Acaraspora schleicheri*, Figure 40). In contrast to cyanolichen, which require liquid water uptake, these lichens can sustain themselves on water vapor (Pointing and Belnap 2012). Thus, they are more abundant and diverse in coastal habitats or in chaparral systems.

Cyanobacterial lichen crusts (cyanolichen crust)

Cyanolichen crusts are associations of fungi and cyanobacteria (Figures 31-35). The lichen thallus is either gelatinous (ridged and wrinkly when dry, becoming gelatinous and swollen when wet; i.e., *Collema* spp.; Figures 31 and 32) or crustose (tightly connected to the soil surface; i.e., *Peltula* spp., *Heppia* spp.; Figures 33 and 34). The thallus of soil cyanolichens in the Mojave Desert is generally darkly pigmented (black, or olive green) (Figures 31-35). Cyanolichens in chaparral systems can be either dark or colorful. In contrast to stratified phycolichens, *Collema* spp. have unstratified thalli (i.e. the stratification into a white fungal layer and a green algal layer is not present) (Belnap et al., 2003).

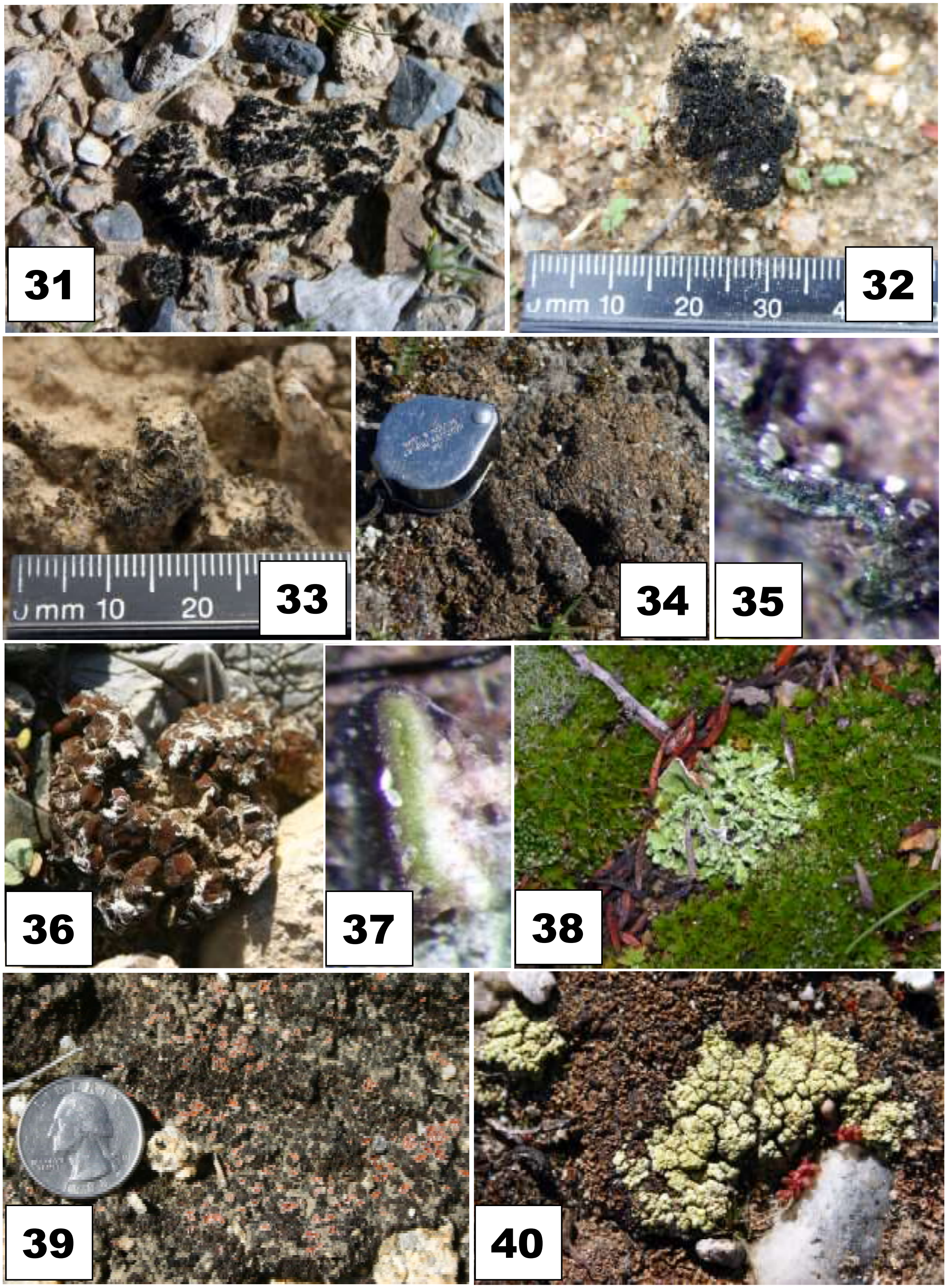
Ecological functions

Lichens contribute greatly to soil stability with their dense network of fungal rhizomorphs, i.e rhizines and hyphae extending into the surface soil (Belnap et al., 2003). Therefore, lichens, together with mosses, have the greatest resistance to wind and water erosion (Belnap & Eldridge 2003) and exhibit the highest degree of soil aggregation (Pietrasiak et al., 2013).

Mosses and lichens are most efficient in carbon fixation, with the highest net photosynthesis of all crust types due to higher chlorophyll-*a* content per area (Lange 2003). The carbon input for lichen and mosses has been estimated to be 1-32 gC m^{-2} per year (Lange et al., 2003, Ebert et al., 2012). Rates of carbon fixation by lichen crusts range from 1.79 to 5.9 µmol CO_2 m^{-2} s^{-1} for green algal lichen *Clavicidium lacinulatum* crusts and 2.49 to 10.89 µmol CO_2 m^{-2} s^{-1} for cyanolichen *Collema coccophorum* crusts collected in the Mojave Desert (Pietrasiak 2012, Pietrasiak et al., 2013). Among all crust community types cyanobacterial lichen crusts are the most efficient crust type to fix nitrogen, especially if nitrogen is limited in the surface soil. Nitrogen fixation rates of 2.4×10^{-1} nmol N_2 m^{-2} h^{-1} (Colorado Plateau, Belnap 1996) to 8.3×10^{-4} nmol N_2 m^{-2} h^{-1} (Mojave Desert, Pietrasiak et al., 2013) have been reported (reviewed in Pietrasiak 2012). The biologically fixed nitrogen is incorporated into crust biomass resulting in an elevation of the total nitrogen content.

Lichen crusts efficiently trapp dust due to their morphologically complex thalli protruding above the soil surface as well as ridges and cracks between the thalli which create microscale differences in topography. In addition, lichen thalli have a high water-holding capacity (Belnap et al., 2003, Evans & Lange 2003). Water content is especially high in gelatinous lichen crusts containing *Collema* spp. (the most common soil lichen crusts in the Mojave Desert) and foliose-fruticose *Cladonia* spp. (common soil lichens among coastal soil crusts*).* Higher water-holding capacity and longer water retention result in longer photosynthesis and respiration which impacts carbon cycling (Evans & Lange 2003).

Figures 31-40. 31) gelatinous cyanolichen *Collema tenax* dry; 32) cyanolichen *Collema tenax,* wet; 33) crustose cyanolichen *Heppia* sp.; 34) crustose cyanolichen *Peltula patellata;* 35) cross section close up of blue-green cyanolichen thallus; 36) squamulous green algal lichen *Placidium lacinulatum*; 37) cross section close up of a green algal lichen thallus; 38) *Cladonia* sp. a coastal and chaparral soil lichen; 39) green algal lichen *Psora decipiens*; 40) rare green algal lichen *Acaraspora schleicheri* from chaparral soil crusts.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Bryophyte crusts

Bryophyte crusts containing mosses and liverworts have the highest moisture requirement among all crust community types. Consequently they are indicators of relatively moist habitats (Belnap et al., 2003). Especially, liverwort crusts are sensitive to moisture availability. Thus, bryophyte crusts are a common crust component of the chaparral and the coastal sage scrub ecosystems where moisture is more abundant and available longer than in the hot deserts of southern California. *Bryum* spp. make up smooth moss crusts, *Syntrichia* spp. are commonly found in roughened moss crusts, and *Crossidium* spp. and *Pterygoneurum* spp. can form hairy moss crusts. Liverwort crusts contain various species of the genus *Riccia*.

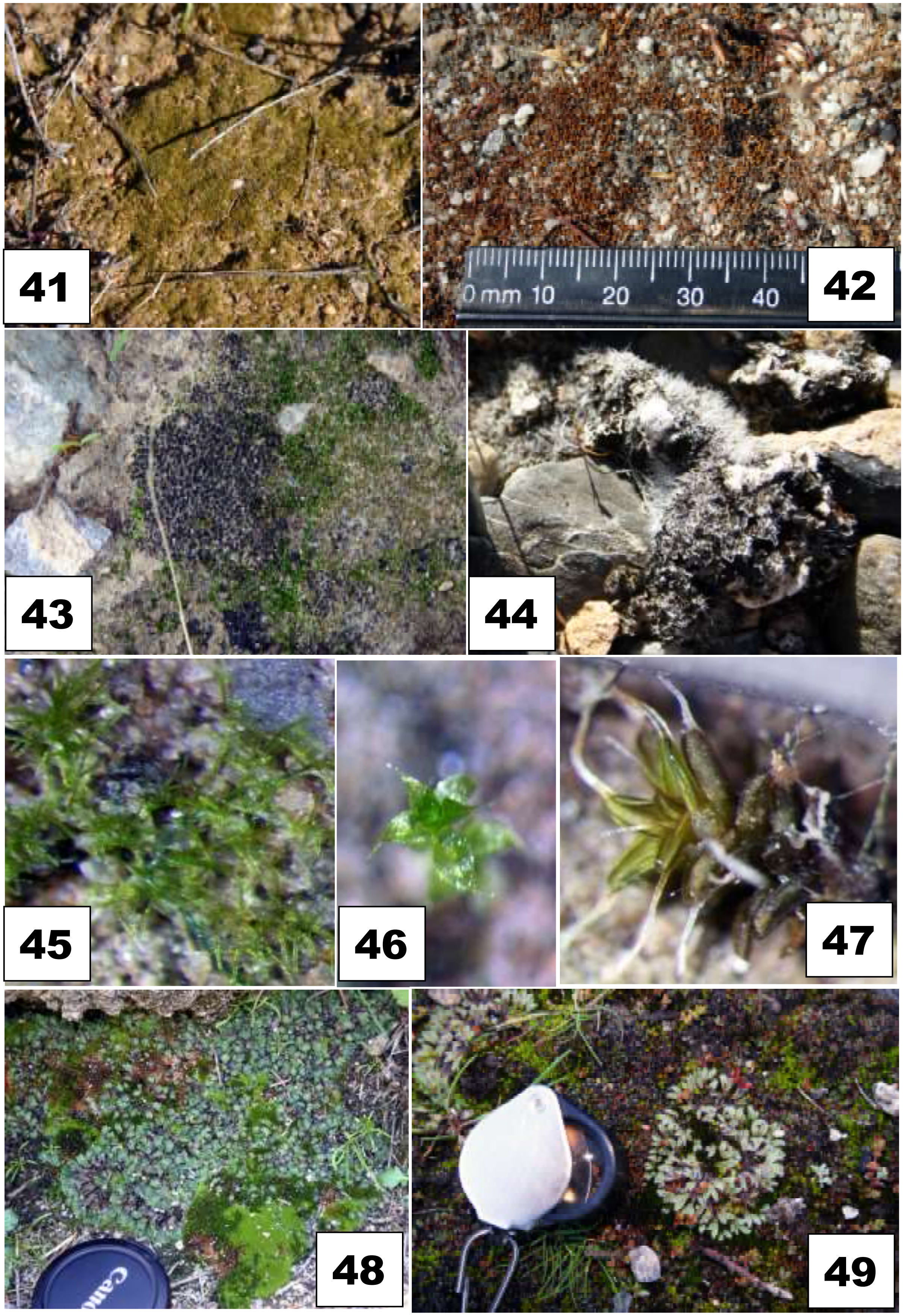
Ecological functions

Similar to lichen crusts, moss crusts affect surface topography and its associated processes because their thallus morphology roughens the surface. In particular, the roughened and hairy moss crusts enhance entrapment of fine particles. Consequently, clay and silt content in the surface soil increases, resulting in an improvement of water-holding capacity and nutrient status. In addition, mosses greatly increase soil aggregate stability by virtue of their rhizoids and protonemata (Belnap et al., 2003, Pietrasiak et al., 2013). Moss crusts may also be more resistant to burial by sediment. Mosses can grow up through the freshly deposited sediment when buried surficially (Danin & Gaynor 1991, Belnap et al., 2003, Jia et al., 2008).

Carbon fixation rates by bryophyte crusts can be among the highest when comparing all crust community types. Rates range from 1.17 to 9.04 µmol CO_2 m^{-2} s^{-1} for bryophytes in Southern California (Pietrasiak 2012, Pietrasiak et al., 2013). Bryophytes themselves are incapable of fixing nitrogen. However, cyanobacteria are often associated within the bryotphyte crust communities and contribute significantly to nitrogen fixation (Zhao et al., 2010). Fixation rates of moss crusts can range from 6.8 x 10^{-2} nmol N_2 m^{-2} h^{-1} (Gurbantungut Desert, China) to 8.7 x 10^{-5} nmol N_2 m^{-2} h^{-1} (Tenger Desert, China, reviewed in Pietrasiak 2012). Liverwort crusts in arctic tundra are reported to fix 9.0 x

10^{-3} nmol N_2 m^{-2} h^{-1}. In the Mojave Desert roughened moss crusts fixed in average 2.7 x 10^{-3} nmol N_2 m^{-2} h^{-1}, where as dark moss crusts fixed in average 7.2 x 10^{-3} nmol N_2 m^{-2} h^{-1}.

Figures 41-49. 41) smooth moss crust; 42) roughened moss crust; 43) blackened moss crust; 44) hairy moss crust; 45) protonemata; 46) close up of roughened moss thallus; 47) moss thallus with hairlike extensions; 48 and 49) liverwort *Rhiccia* spp.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GLOSSARY

Albedo – is the reflecting electromagnetic radiation of a surface

Algae – include eukaryotic and prokaryotic photosynthetic organisms that contain chlorophyll

Bryophytes – non-vascular land plants that include mosses and liverworts

Crustose – tile-like lichen growth form that is firmly attached to the soil with entire thallus

Cyanobacteria – prokaryotic organisms capable of photosynthesis (i.e. carbon fixation), appear bluegreen in color

Dichotomous – divided into two parts

Eukaryotic – taxanomic domain of organisms unified by presence of a nucleus and membrane bound organelles

Eukaryotic soil algae – eukaryotic algae that include diatoms, chlorophytes, tribophytes, eustigmatophytes

Extracellular polysaccharides – sugars that have been secreted outside of the cell which are often of sticky consistency and aid in soil aggregation

Filament – microscopic string- or thread-like structure developed by cyanobacteria, fungi, or mosses. If soil crust is lifted, filaments often can be seen as very fine threads hanging off the crust with attached soil particles

Smooth crust morphology – flat surface morphology of the crust

Foliose – leaf-like lichen growth form

Fruticose – intricately branched or hair-like lichen growth form

Fungus/Fungi – heterotrophic eukaryotic organisms

Gelatinous – jelly-like, rubbery lichen growth form, especially conspicuous when moist

Heterocytes – specialized cyanobacterial cells capable of fixing nitrogen

Heterotrophic – requiring external organic nutrition; not photosynthetic or chemoautotrophic

Hypha/Hyphae – often white or translucent, branching filaments of fungi or actinobacteria, vegetative growth structure

Incipient – in beginning stage or beginning to be noticeable

Lichen – mutualistic association of fungus and algae living in symbiosis to the benefit of each member involved

Photosynthesis – a biochemical process of chlorophyll containing organisms to produce carbohydrates and release oxygen by fixing carbon dioxide from the atmosphere and taking water up from the environment

Phyllid – leaf-like structure of bryophytes

Prokaryotic algae – bluegreen algae also known as cyanobacteria; lack membrane-bound organelles

Protonemata (singular Protonema) – primitive filamentous structure that germinates out of a moss spore and eventually develops into the leaf-like moss thallus

Rhizines – root-like filaments of lichens

Rhizoids – root-like filaments of bryophytes

Rhizomorphs – root-like filaments of fungi

Rugose crust morphology – roughened surface morphology of the crust

Squamulous – scaly or cornflake-like lichen growth form

Symbiont –an organism that is part of a mutualistic relationship

Symbiosis –a close relationship of two or more organisms living together

Thallus/ (plural Thalli) – primitive vegetative growing body of lichen and bryophytes

Reference Cited

Belnap, J. & Gardner, J.S. (1993): Soil microstructure of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53: 40-47.

Belnap, J. (1996): Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. Biology and Fertility of Soils 23:362-367.

Belnap, J., Kaltenecker, J.H., Rosentreter, R., Williams, J., Leonard, S. & Eldridge D.J. (2001): Biological soil crusts: Ecology and management: TR–1730-2, US Department of the Interior, Denver, CO.

Belnap, J., Büdel, B. & Lange, O.L. (2003): Biological soil crust: characteristics and distribution. In: Belnap, J. & Lange, O.L. (eds): Biological soil crusts: Structure, function, and management. Rev. 2nd print. Berlin.

Danin, A. & Gaynor, E. (1991): Trapping of airborne dust by mosses in the Negev Desert, Israel. Earth Surface Processes and Landfroms 16: 153-162.

Darby, B.J., Neher, D.A. & Belnap, J. (2007): Soil nematode communities are ecologically more mature beneath late- than early-sucessional stage biological soil crusts. Applied Soil Ecology 35: 203-212.

Belnap, J. & Eldridge, D.J. (2003): Disturbance and recovery of Biological Soil Crust. In: Belnap, J. & Lange, O.L. (eds): Biological soil crusts: Structure, function, and management. Rev. 2nd print. Berlin.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O. & Pöschl, U. (2012): Contribution of cryptogamic coversto the global cycles of carbon and nitrogen. Nature Geoscience 5: 459-462.

Eldridge, D.J. & Rosentreter, R. (1999): Morphological groups. A framework for monitoring microphytic soil crust in relation to indices of landscape health. Journal of Arid Environments 41: 11-25.

Evans, R.D. & Johansen, J.R. (1999): Microbiotic crusts and ecosystem processes. Critical Reviews in Plant Sciences 18: 183-225.

Evans, R.D. & Lange, O.L. (2003): Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap, J. & Lange, O.L. (eds): Biological soil crusts: Structure, function, and management. Rev. 2nd print. Berlin.

Jia, R.L., L, X.R., Liu, L.C., Gao, Y.H. & Li, X.J. (2008): Responses of biological soil crusts to sand burial in a revegetated area of the Tengger Desert, Northern China. Soil Biology & Biochemistry 40: 2827-2834.

Johansen, J.R. (1993): Cryptogamic crusts of semiarid and arid lands of North America. Journal of Phycology 29: 140-147.

Johansen, J.R. & Schubert, L.E. (2001): Algae in soils. Nova Hedwigia, Beiheft 123: 297-306.

Lange, O.L. (2003): Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap, J. & Lange, O.L. (eds): Biological soil crusts: Structure, function, and management. Rev. 2nd print. Berlin.

Navaro, J.B, Moser, D.P., Flores, A., Ross, C., Rosen M.R., Dong, H., Zhang, G. & Hedlund, B.P. (2009): Bacterial succession within an ephemeral hypereutrophic Mojave Desert Playa Lake. Microbiol Ecology 57: 307-320.

Nübel, U., Garcia-Pichel, F., Kühl, M. & Muyzer, G. (1999): Quantifying microbial diversity: Morphotypes, 16S rRNA genes, and carotenoids of oxygenic phototrophs in microbial mats. Apllied and Environmental Microbiology 65: 422-430

Pietrasiak, N. (2005): Spatial assessment of microbiotic soil crust in high vs. low recreational use areas within the Wonderland of Rocks of Joshua Tree National Park, California. Diploma Thesis. University of Leipzig. Germany. 94 pp.

Pietrasiak, N., Johansen, J.R. & Drenovsky, R.E. (2011): Geologic composition influences distribution of microbiotic crusts in the Mojave and Colorado Deserts at the regional scale. Soil Biology and Biochemistry 43: 967-974.

Pietrasiak, N. (2012): Effects of land surface characteristics on pedogenesis, biological soil crust community diversity, and ecosystem functions in a Mojave Desert piedmont landscape. Ph.D. Dissertation. University of California, Riverside., U.S.A. 208 pp.

Pietrasiak, N., Regus, J.U., Johansen, J.R., Lam, D., Sachs, J.L. & Santiago, L.S. (2013): Biological soil crust community types differ in key ecological functions. Soil Biology and Biochemistry 65: 168-171.

Pietrasiak, N., Drenovsky, R.E., Santiago, L.S., & Graham, R.C. (2014): Biogeomorphology of a Mojave Desert Landscape – configurations and feedbacks of abiotic and biotic land surfaces during landform evolution. Geomorphology 206: 23-36.

Pointing, S.B. & Belnap, J. (2012): Microbial colonization and controls in dryland systems. Nature Reviews Microbiology 10: 551-562.

Shepherd, U.L., Brantley, S.L. & Tarleton, C.A. (2002): Species richness and abundance patterns of microarthropods on cryptobiotic crusts in a piñon – juniper habitat: a call for greater knowledge. Journal of Arid Environment 52: 349-360.

St. Clair, L.L. & Johansen, J.R. (1993): Introduction to the symposium on soil crust communities. Great Basin Naturalist 53: 1-4.

Su, Y.G., Zhao, X., Li, A.X., Li, X.R. & Huang, G. (2011): Nitrogen fixation in biological soil crusts from the Tengger desert, northern China. European Journal of Soil Biology 47: 182-187.

Valentin, C. (1991): Surface crusting in two alluvial soils of northern Niger. Geoderma 48: 201-222.

Valentin, C. & Bresson, L.-M. (1992): Morphology, genesis and classification of surface crusts in loamy and sandy soils. Geoderma 55: 225-245.

West, N.E. (1990): Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Adv. Ecol. Res. 20: 45-53.

Williams, A.J., Buck, B.J. & Beyene, M.A. (2012): Biological soil crusts in the Mojave Desert, USA: Micromorphology and pedogenesis. Soil Science Society of America Journal 76: 1685-1695.

Wood, M.K., Eckert, R.E. JR, Blackburn, W.H. & Peterson, F.F. (1982): Influence of crusting soil surfaces on emergence and establishment of crested wheatgrass, suirreltail, Thurber needlegrass, and fourwing saltbush. Journal of Range Management 35: 282-287.

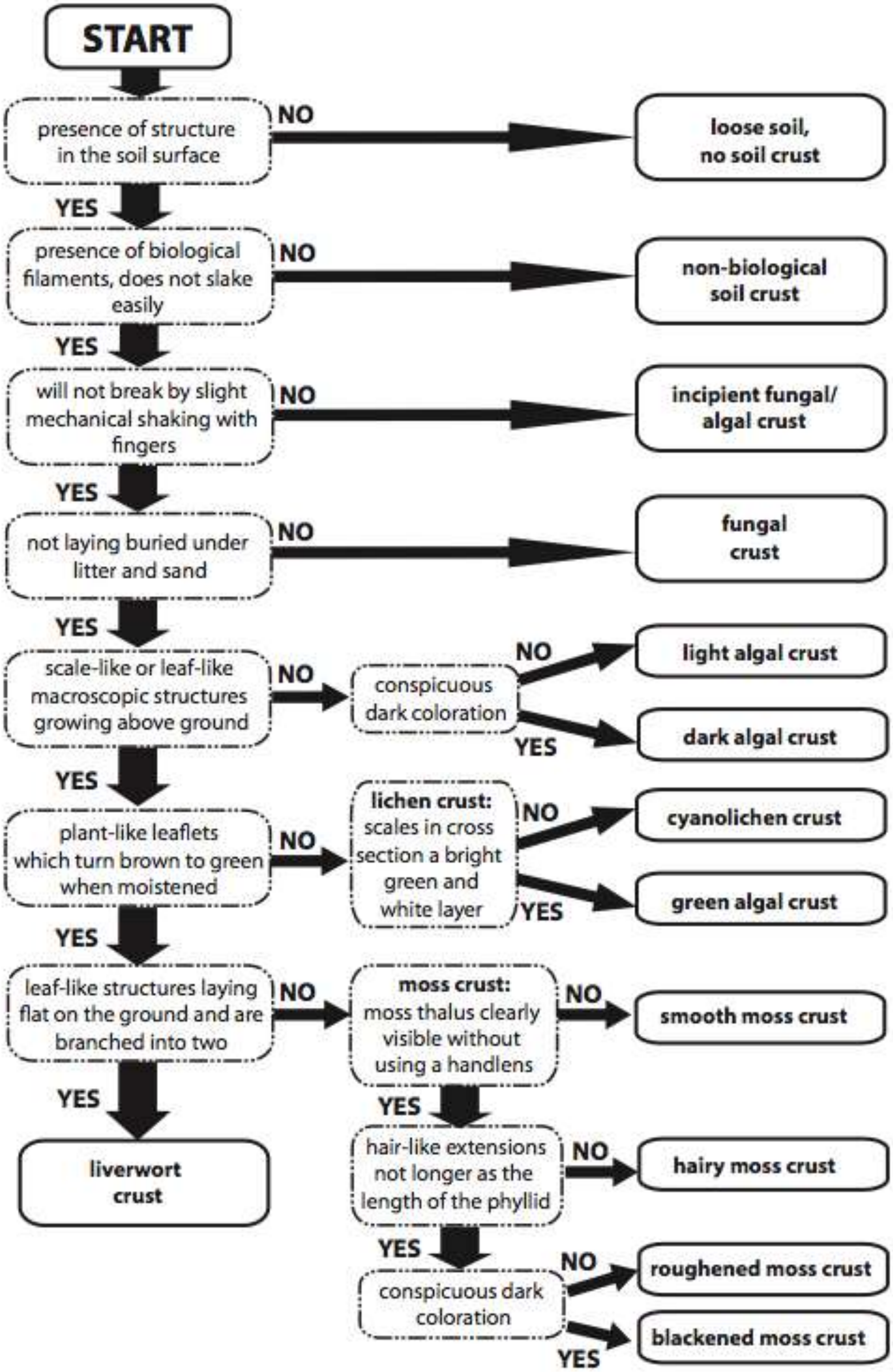
Wood, Y.A., Graham, R.C. & Wells, S.G. (2005): Surface control of desert pavement pedological process and landscape function, Cima Volcanic field, Mojave Desert, California. Catena 59: 205-230.

Zaady, E., Groffman, P. & Shachak, M. (1998): Nitrogen fixation in macro- and microphytic patches in the Negev Desert. Soil Biology and Biochemistry 30: 449-454.

Zaady, E. & Bouskila, A. (2002): Lizard burrows association with successional stages of biological soil crusts in an arid sandy region. Journal of Arid Environments 50: 235-246.

Zhao, Y., Xu, M. & Belnap, J. (2010): Potential nitrogen fixation activity of different aged biological soil crusts from rehabilitated grasslands of the hilly Loess Plateau, China. Journal of Arid Environments 74: 1186-1191.

Figure 50. Quick-reference flow chart for identification of biocrust community types.


START
presence of structure in the soil surface
NO
loose soil, no soil crust
YES
presence of biological filaments, does not slake easily
NO
non-biological soil crust
YES
will not break by slight mechanical shaking with fingers
NO
incipient fungal/ algal crust
YES
not laying buried under litter and sand
NO
fungal crust
YES
scale-like or leaf-like macroscopic structures growing above ground
NO
conspicuous dark coloration
NO
light algal crust
YES
dark algal crust
YES
plant-like leaflets which turn brown to green when moistened
NO
lichen crust: scales in cross section a bright green and white layer
NO
cyanolichen crust
YES
green algal crust
YES
leaf-like structures laying flat on the ground and are branched into two
NO
moss crust: moss thalus clearly visible without using a handlens
NO
smooth moss crust
YES
liverwort crust
YES
hair-like extensions not longer as the length of the phyllid
NO
hairy moss crust
YES
conspicuous dark coloration
NO
roughened moss crust
YES
blackened moss crust